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MINI-REVIEW

Advances in microbial pretreatment for biorefining of perennial grasses

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Abstract

Perennial grasses are potentially abundant sources of biomass for biorefineries, which can produce high yields with low input requirements, and many added environmental benefits. However, perennial grasses are highly recalcitrant to biodegradation and may require pretreatment before undergoing many biorefining pathways. Microbial pretreatment uses the ability of microorganisms or their enzymes to deconstruct plant biomass and enhance its biodegradability. This process can enhance the enzymatic digestibility of perennial grasses, enabling saccharification with cellulolytic enzymes to produce fermentable sugars and derived fermentation products. Similarly, microbial pretreatment can increase the methanation rate when the grasses are used to produce biogas through anaerobic digestion. Microorganisms can also increase the digestibility of the grasses to improve their quality as animal feed, enhance the properties of grass pellets, and improve biomass thermochemical conversion. Metabolites produced by fungi or bacteria during microbial pretreatment, such as ligninolytic and cellulolytic enzymes, can be further recovered as added-value products. Additionally, the action of the microorganisms can release chemicals with commercialization potential, such as hydroxycinnamic acids and oligosaccharides, from the grasses. This review explores the recent advances and remaining challenges in using microbial pretreatment for perennial grasses with the goal of obtaining added-value products through biorefining. It emphasizes recent trends in microbial pretreatment such as the use of microorganisms as part of microbial consortia or in unsterilized systems, the use and development of microorganisms and consortia capable of performing more than one biorefining step, and the use of cell-free systems based on microbial enzymes.

Key points

- *Microorganisms or enzymes can reduce the recalcitrance of grasses for biorefining*
- *Microbial pretreatment effectiveness depends on the grass-microbe interaction*
- *Microbial pretreatment can generate value added co-products to enhance feasibility*

Keywords Energy crops · Biomass · Fractionation · Fungal pretreatment · Bioproduct · Enzyme

Introduction

The bioeconomy requires abundant sources of biomass that can be converted into food, feed, bioenergy, and biomaterials to replace those currently obtained from fossil fuels. Perennial grasses are resilient, fast-growing plants, with high yields, and very low input requirements, which make them an important source of biomass for biorefining. Recently, perennial grasses have gained significant attention over other biomass sources due to their high biomass yields, potential for carbon and nutrient sequestration in their roots, and additional soil, habitat, and biodiversity benefits (Brandes et al. 2018; Dahmen et al. 2019; Scordia and Cosentino 2019; Field et al. 2020; He et al. 2022). In addition, perennial grasses have fewer logistic and ecological collection

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constraints as compared with agricultural residues (Bentsen et al. 2014; Wang et al. 2021c).

Perennial grasses are composed of lignocellulose and cell contents such as sugars, proteins, lipids, and minerals (Bichot et al. 2018). Most biorefineries use lignocellulose to manufacture biobased products. However, accessing the lignocellulose in the grasses presents unique challenges due to the highly variable structure of plant tissues and their natural protection against biodegradation, often referred to as recalcitrance (Bichot et al. 2018). To overcome these challenges, pretreatment processes that modify the physical and chemical structure of the lignocellulose and enhance the accessibility of the desired biomass fractions are required for most biorefinery applications of perennial grasses (Mohapatra et al. 2017; Rodriguez et al. 2017). Pretreatment processes can easily become the bottleneck of the biorefinery due to their potential high costs, energy usage, and process impediments of this industrial heterogeneous process that uses a feedstock with high bulk density and low flowability, such as grass (Mosier et al. 2005; Senturk-Ozer et al. 2011).

As an alternative to traditional pretreatments, the use of microorganisms and their enzymes to pretreat herbaceous biomasses has been extensively studied. Microbial pretreatments use a variety of microorganisms that are capable of enhancing the biodegradability of the grasses, generating a feedstock that is more amenable to biorefining. Microbial pretreatments take advantage of the powerful enzymatic systems of fungi and bacteria and thus are performed under mild environmental conditions and with little or no added chemicals (Sindhu and Pandey 2016; Vasco-Correa et al. 2016a). However, the implementation of microbial pretreatment has been constrained by the long processing times, limitations in its effectiveness, and uncertainties regarding scalability and economic feasibility (Vasco-Correa et al. 2019b).

In this review, we aim to summarize recent advances in microbial pretreatment approaches that enhance the digestibility of perennial grasses for use as a biomass source in biorefining. We focus on perennial grasses specifically, and not annual crops, for the high biomass yields and environmental benefits. We make a strong emphasis on perennial grasses that are dedicated energy crops, with less attention to food crops. For this, we reviewed the scientific literature on the topic indexed on the Scopus database, with a particular emphasis on papers published on or after 2010, using both general keywords and specific species of perennial grasses. We critically review microbial pretreatment approaches and their effectiveness for perennial grasses that are further processed into sugars and derivative products, biogas through anaerobic digestion, and animal feed. We discuss new approaches of using cell-free enzymatic systems, natural and designed microbial consortia, and consolidated processes that include microbial pretreatment, as well as novel applications of microbial pretreated materials such as biomass densification, enzyme production, and fractionation of high-value chemicals.

Perennial grasses

Grasses, or *Gramineae* plants, can be annual or perennial. Perennial grasses are mostly forage grasses, while annual grasses include most cereal crops. Annual grasses, like any other annual crop, must be planted every year, while perennial grasses, once established, can be harvested at least once a year with no additional planting efforts (Lewandowski et al. 2003).

Grasses are composed of cell contents and cell wall components. Cell contents include free sugars, proteins, lipids, and minerals, while cell wall components are mostly cellulose, hemicellulose, and lignin. The cell wall is more recalcitrant to biodegradation while the cell contents are more digestible and easier to extract with solvents (Rodriguez et al. 2017). Perennial grasses produce a significant amount of above-ground biomass, composed of leaves, stalks, and nodes which can all be harvested and used in biorefineries. Stalks are high in cell wall components, while the leaves are rich in cell content. Although grasses are considered lignocellulosic biomass, they have a different chemical composition than woody biomasses, with a lower lignin and a higher holocellulose (cellulose plus hemicellulose) content. Perennial grasses also have an extensive root system (rhizomes), which extends with maturity and allows carbon fixation in the soil and nutrient remobilization (Scordia and Cosentino 2019).

Perennial grasses usually have low fertilizer requirements, mostly because they have the capacity to remobilize nutrients to their rhizomes at the end of the growing season. This advantage is seen mostly when the grass is harvested after senescence (Kering et al. 2012). Most perennial grasses can be harvested once or twice per year but harvesting more than once reduces the nutrient efficiency of the grasses. The harvest time can also affect the composition of the cell contents and cell walls, since the cell wall components increase with maturity, while the cell contents decrease. In addition, leaving the grass for longer in the field usually results in biomass loss, mostly in the form of fallen leaves. Thus, a later harvest time usually implies higher lignin content and lower digestibility (Seppälä et al. 2009). The variability in composition with grass maturity and harvesting time represents a challenge for the biorefining processes, since the composition of the grasses will directly affect their use and conversion efficiencies (Bichot et al. 2018).

Perennial grasses are classified according to their growth temperature and photosynthetic pathway. C4 grasses, which follow a C4 cycle for the incorporation of carbon dioxide,

grow in tropical weather and are more efficient than C3 grasses. They are also known as warm-season grasses and grow better during summer. Their photosynthesis pathway requires more ATP, but also fixes more carbon dioxide and has a higher potential for carbon sequestration. C3 grasses are adapted to grow in more temperate weather and thus are known as cool-season grasses. They grow better in fall or spring (Bichot et al. 2018). C4 grasses usually generate higher biomass yields and are more tolerant of drought and heat stress (Ge et al. 2016).

Grasses can also be classified as thin- or thick-stemmed. Thin-stemmed grasses are easier to harvest with traditional hay equipment, while thick-stemmed grasses usually require forage harvesters or other specialized equipment. Thick-stemmed perennial grasses are mostly C4 tropical grasses such as *Saccharum* species (e.g., sugarcane and energy cane), *Miscanthus*, and Napier grass. Thin-stemmed grasses include both warm-season grasses (e.g., switchgrass and eastern gama grass), and cool-season grasses, such as Timothy grass and reed canary grass (Brown and Brown 2014).

Planting perennial grasses has many other added benefits. The low nutrient requirements and efficient water use allow many of these grasses to grow in marginal lands. Furthermore, they have the potential to restore these lands, since their growth promotes carbon fixation in the soil, and they can absorb heavy metals and other contaminants (Nsanganwimana et al. 2014; Clifton-Brown et al. 2017). Many perennial grasses, mostly warm-season grasses, have a very efficient use of water and are draught tolerant (Bichot et al. 2018). They can improve water quality, mitigate nitrate-nitrogen leaching, and prevent erosion (Brandes et al. 2018). They increase biodiversity since they create habitats for flora and fauna, which correlates with other ecosystem services such as mitigation of methane emissions, pest suppression, and pollination (Werling et al. 2014).

Common perennial grasses in biorefining

Many perennial grasses have been studied for biorefining, including both C3 and C4 grasses. Some of the most common ones include switchgrass, *Miscanthus*, and giant reed. Switchgrass (*Panicum virgatum*) is a C4 grass that was selected in the United States as the model perennial grass in the 1990s (Parrish et al. 2012). It is native to North America, and it is easier to propagate than other perennial grasses such as *Miscanthus*, achieving yields of up to 20–25 MT/ha (Larnaudie et al. 2022). Switchgrass has a high cellulose content of 30–44% (dry matter based) and has been extensively used for forage, erosion control, and to reduce nutrient runoff (Parrish et al. 2012; Larnaudie et al. 2022).

Miscanthus is a genre of perennial C4 grasses of East Asian origin that include the popular sterile hybrid *Miscanthus* x *giganteus* (giant miscanthus). *Miscanthus* has been studied not only for its high yields, which can reach over 40 MT/ha, but also for its capacity for phytoremediation and to grow in marginal lands with little inputs (Wang et al. 2021a), and its adaptability to different climates (Clifton-Brown et al. 2017). *Miscanthus* has a high cellulose content that can reach 50% of its dry matter when harvested as a mature crop in the spring (Lee and Kuan 2015). Its establishment and propagation are challenging because it requires rhizomes, which are slow to produce and plant, require a lot of land for their generation, and are sensitive to stressors (Shepherd et al. 2023). After the crop has been established, it can last up to 25 years (Anderson et al. 2011).

Giant reed (*Arundo dunax*) is an invasive species of C3 grass that originated in East Asia and has a high growth rate and biomass yields, especially in soils rich in water (Corno et al. 2014). Giant reed is a sterile grass, but can reproduce vegetative, which enables its invasiveness. This grass has a high growth rate, closer to that of a C4 grass, and can achieve 60 MT/ha of biomass and up to two harvests per year (Ge et al. 2016). Its establishment can be expensive due to its sterility and high water requirements during the first year (Pilu et al. 2013), and the crop can last up to 15 years (Angelini et al. 2009).

Other common grasses studied include Napier grass and Bermuda grass. Napier grass (*Pennisetum purpureum*) is a C4 grass native to eastern and central Africa that produces yields up to 60 MT/ha and can grow well in soils with limited nitrogen (Mohapatra et al. 2017). Napier grass grows well in warm and subtropical regions and produces a steady biomass supply with a relatively consistent composition through its growth cycle (Takara and Khanal 2015). Bermuda grass (*Cynodon dactylon*) is a C4 grass that grows in tropical and subtropical regions with a yield of up to 25 MT/ha and is grown in the Southern United States for hay and forage (Xu et al. 2011).

Pretreatment of perennial grasses

The lignocellulose of perennial grasses can be a great resource for biorefining. A wide range of biobased products can be produced from the different fractions of the lignocellulose, for applications in the bioenergy, biomaterials, and biochemicals sectors. However, accessing the different fractions can be a challenge, since perennial grasses are highly recalcitrant to biodegradation (Bichot et al. 2018).

The recalcitrance of the grass cell wall is mostly due to the presence of lignin, the crystallinity of cellulose, and the intricate structure formed by the interactions between these polysaccharides and aromatic polymers (Bichot et al. 2018). Grasses have abundant esterified phenolic acids such as p-coumaric and ferulic acid linked to polysaccharides, which have been associated with their lack of biodegradability (Akin 2007). These ester links are more common in

warm-season grasses (Anderson and Akin 2008). Lignin is a heteropolymer that in grasses is mainly composed of guaiacyl (G) and syringyl (S) units and that acts as support for plant growth and as a physical barrier to biodegradation (Rodriguez et al. 2017). Lignin content is directly related to the enzymatic digestibility of the polysaccharides in grasses (Saballos et al. 2008; Costa et al. 2013; Vasco-Correa et al. 2016b, 2022). However, recent studies have also shown that the allocation of the lignin and its modifications are equally important in the recalcitrance of grasses (Yan et al. 2015; Yang and Pan 2016). Hemicellulose in grasses is rich in glucuronoarabinoylan and arabinoglucuranoxylan.

Pretreatment and fractionation processes have been developed to reduce the recalcitrance of the lignocellulosic biomass and allow access to the different fractions in the biorefinery conversion processes. Pretreatment processes use a combination of added chemicals, temperature, pressure, and mechanical stressors to alter the structure of the cell wall components of the grasses, resulting in a residual biomass that is more amenable to conversion into biobased products. These conditions often require intensive energy use for the pretreatment or for the recycling of chemicals and can be expensive and operationally cumbersome (Mosier et al. 2005). Pretreatment has been adapted to many applications of the grasses, such as the production of renewable natural gas through anaerobic digestion, production of fermentable sugars that could be converted into liquid fuels and chemicals, enhancing the digestibility of the biomass for feed uses, and other biochemical and thermochemical conversion processes of biomass into chemicals and materials.

Microbial pretreatment of perennial grasses

To counteract some of the disadvantages of traditional pretreatments, alternative pretreatments using microorganisms have been proposed. Microbial pretreatments use the capacity of microorganisms to grow in the grasses and degrade certain components, altering the structure of the cell wall components. Microbial pretreatments use specific fungi, bacteria, or complex microbial consortia, or they can also use the enzymatic extract produced by these microorganisms, in what is known as enzymatic pretreatment.

Fungal pretreatment is the most common microbial pretreatment, and it is based on the ability of fungi to grow in biomass and alter its composition and structure. Most fungal pretreatments use wood decay fungi, which are saprophytic fungi that are part of the carbon cycle of wood (Sista Kameshwar and Qin 2018). Thus, these fungi are better adapted to woody biomass and sometimes underperform when grown in herbaceous materials (Kaffenberger and Schilling 2013; Vasco-Correa et al. 2019a). Fungal pretreatment is generally performed in solid state with no free water, and without added chemicals at mild temperatures, which makes it compatible with wet storage of biomass. The main mechanisms of fungal pretreatment are oxidative reactions, and thus the system requires aerobic conditions.

After microbial pretreatment, grasses are more amenable to biorefining in different processes. Their digestibility and biodegradability highly improve, and they can be sent to enzymatic saccharification with cellulolytic enzymes to produce sugars, which can be later converted through fermentation into liquid fuels and chemicals. The improved digestibility also helps improve their methanation in anaerobic digestion systems to produce renewable natural gas (RNG), and favors their use as enhanced animal feed. The structural changes also improve the properties of the material for its conversion into pellets or biochar, and the microbial growth can generate added-value products such as enzymes, hydroxycinnamic acids, and oligosaccharides (Fig. 1).

Microbial pretreatment of grasses for fermentable sugars and derived products

Fermentable sugars from grasses are obtained from the hydrolyzation of the holocellulose fraction of the biomass, which is usually performed with cellulolytic enzymes. However, most grasses are highly recalcitrant to this hydrolysis, and without pretreatment, only around 5–15% of the sugars in the holocellulose can be released under standard conditions (Vasco-Correa et al. 2016b). Thus, pretreatment is required to reduce the recalcitrance of grasses before adding the saccharification enzymes, to ensure a more efficient fermentable sugar production. Physicochemical pretreatments have been widely studied on grasses for sugar-based biorefineries. Successful pretreatment of perennial grasses has been achieved with dilute acid, alkaline, ammonia fiber expansion (AFEX), and liquid hot water pretreatment, among others (Murnen et al. 2007; Digman et al. 2010; Li et al. 2013; Zhao et al. 2017a).

Microbial pretreatment has been researched extensively for the fractionation of lignocellulosic biomass, with the final objective of increasing the digestibility of the polysaccharide fractions to enzymatic hydrolysis (Vasco-Correa et al. 2016a). Most microbial pretreatments have proven more effective with woody feedstock than with herbaceous feedstocks (Vasco-Correa et al. 2019a); however, successful pretreatments have been developed for certain grasses (Table 1).

Fungal pretreatment is the most common technique of microbial pretreatment, based on the capacity of certain fungi to degrade biomass components. All the microorganisms listed in Table 1 belong to the fungi kingdom. Among all the culturable fungi, white rot fungi are by far the most used microorganisms for biomass pretreatment (Table 1). White rot fungi are wood decay fungi with an extraordinary

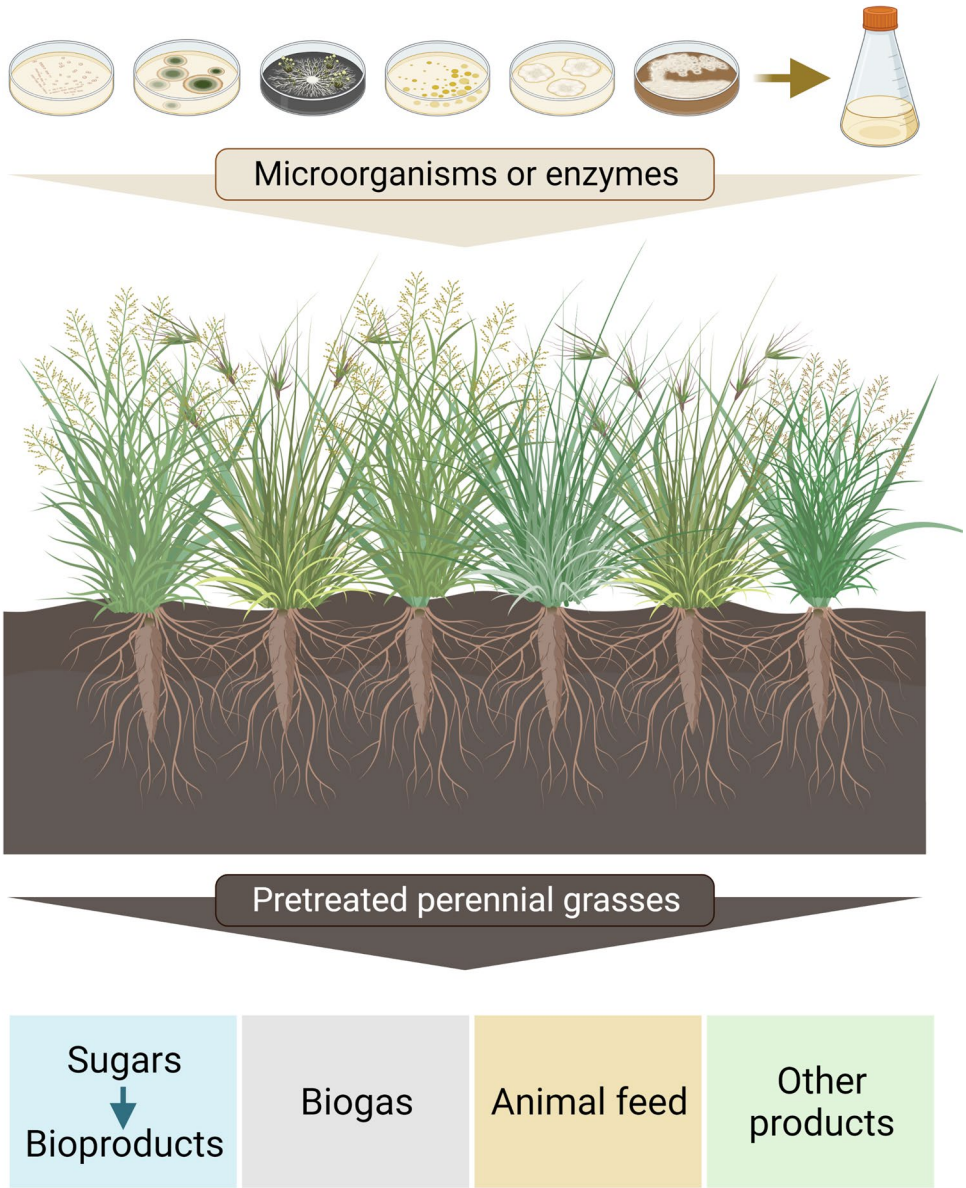

Fig. 1 Perennial grasses can be pretreated with microorganisms or their enzymes for biorefining into fermentable sugars, biogas, animal feed, or other added-value products such as enzymes, hydroxycinnamic acids, and oligosaccharides. Created with BioRender.com

ability to degrade lignin, thanks to their ligninolytic enzyme system, which can include a combination of lignin peroxidases, laccases, manganese peroxidases, versatile peroxidases, dye-decolorizing peroxidases, and accessory enzymes (Kumar and Chandra 2020). They can metabolize part of the lignin as a carbon and energy source (del Cerro et al. 2021). Fungi will simultaneously degrade the polysaccharides in the biomass and use them as an additional carbon and energy source. However, certain white rot fungi are considered selective degraders of lignin, since they degrade lignin with minimal cellulose loss. The selective degrader white rot fungus *Ceriporiopsis subvermispora* has been used to enhance the enzymatic digestibility of *Miscanthus* threefold to fourfold, yielding over 50% of the glucose available in the cellulose after 28 days of incubation time (Vasco-Correa et al. 2016b). Similarly, a glucose yield of about 53% was obtained from energy cane after 30 days, reaching a maximum saccharification rate of 67% at 50 days (Cao 2016). A glucose yield of around 40% was observed under similar conditions for switchgrass after 18 days (Wan and Li 2011). Other white rot fungi that are simultaneous—not selective—lignin degraders, such as *Trametes versicolor* and *Phanerochaete chrysosporium*, have also been used for pretreatment of *Miscanthus*, switchgrass, and other grasses, with more limited success (Kalinoski et al. 2017; Olughu et al. 2022).

Albeit these significant increases in enzymatic digestibility of perennial grasses with white rot fungi treatment, the total sugar released is still limited as compared to physicochemical pretreatments, which can consistently release over 90% of the sugars in the pretreated biomass (Galbe

Table 1 Microbial pretreatment of perennial grasses to release fermentable sugars

Grass	Microorganism species	Glucose (or sugar) yield from pretreated grass	Percentage increase in glucose (or sugar) yield	Pretreatment time (d)	Reference
Switchgrass	*Ceriporiopsis subvermispora**	40%	300%	18	(Wan and Li 2011)
	*Agaricus molybdites**	20%	100%	30	(Liu et al. 2015)
	*Phanerochaete chrysosporium**	19%	90%	21	(Olughu et al. 2022)
	*Trametes versicolor**	18%	80%	21	(Olughu et al. 2021)
	Lepiota spp.	14%	37%	30	(Liu et al. 2015)
	Pycnoporus sp. SYBC-L3*	65%	35%	36	(Liu et al. 2013)
	Ligninolytic not identified	12%	22%	30	(Liu et al. 2015)
	Ceriporiopsis spp.*	12%	19%	30	
	Trichoderma spp.	12%	18%	30	
	Ligninolytic not identified	12%	17%	30	
	Lichen spp.	10%	4%	30	
	Aspergillus flavus	10%	0%	30	
Miscanthus	*Ceriporiopsis subvermispora**	52%	550%	28	(Vasco-Correa et al. 2016b)
	*Ceriporiopsis subvermispora**	22%	100%	28	(Vasco-Correa et al. 2019a)
	*Trametes versicolor**	16%	57%	30	(da Costa et al. 2021)
	*Pleurotus ostreatus**	5%	−48%	30	
	*Ganoderma lucidum**	5%	−52%	30	
Giant reed[1]	*Trichoderma koningii*	55%	127%	14	(Majeed et al. 2020)
	Aspergillus niger	46%	90%	14	
	*Pleurotus ostreatus**	13 to 30%	−39 to 26%	30	(da Costa et al. 2021)
	*Ganoderma lucidum**	21 to 22%	−14 to 4%	30	
	*Trametes versicolor**	12 to 18%	−50 to −17%	30	
Sugarcane bagasse	*Sporotrichum thermophile* BJAMDU5	41%	1267%	4	(Bala and Singh 2019)
	*Trametes villosa**	23%	77%	49	(Hartmann et al. 2022)
	*Pleurotus albidus**	16%	23%	49	
	*Schizophyllum comune**	16%	23%	49	
	*Pleurotus pulmonaris**	13%	0%	49	
	*Marasmiellus palmivorus**	4%	−69%	49	
Pampa grass[1]	*Ganoderma lucidum**	19 to 28%	−12 to 0%	30	(da Costa et al. 2021)
	*Trametes versicolor**	16 to 25%	−26 to −10%	30	
	*Pleurotus ostreatus**	11 to 23%	−48 to −20%	30	
Common reed[1]	*Ganoderma lucidum**	22 to 18%	−40 to 1%	30	(da Costa et al. 2021)
	*Pleurotus ostreatus**	8 to 26%	−61 to −10%	30	
	*Trametes versicolor**	16 to 26%	−24 to −12%	30	
Munja grass	*Sporotrichum thermophile* BJAMDU5	46%	2200%	4	(Bala and Singh 2019)

[1]Ranges varied with the grass tissue digested (stem or leaves)

*Confirmed white rot fungus

and Zacchi 2012). Furthermore, unsuccessful fungal pretreatment of grasses has been reported. Da Costa et al. (2021) saw either no change or a decrease in saccharification in most cases of fungal pretreatment of *Arundo donax*, *Cortaderia selloana*, *Phragmites australis*, and *Miscanthus* x *giganteous* with three different white rot fungi. They hypothesized that this decrease was caused by formation of compounds that inhibited the hydrolytic enzymatic action during the fungal treatment (da Costa et al. 2021). Similarly, the glucose yield from *Miscanthus* treated with *Trametes versicolor* was comparable or even lower to that of the untreated materials, unless a chitinase was added to the enzymatic cocktail mix (Kalinoski et al. 2017). Hartmann et al. (2022) saw a decrease in sugar yield from sugarcane bagasse after fungal pretreatment with *Pycnoporus sanguineus* and *Marasmiellus palmivorus*; however,

pretreatment with *Trametes villosa* was able to enhance the cellulose digestibility by 60% as compared to that of the untreated bagasse.

Brown rot fungi are another kind of wood decay fungi that has also been used for fungal pretreatment of biomass. Brown rot fungi lack the capacity to degrade lignin but can enhance the enzymatic digestibility of grasses by degrading hemicellulose and even hydrolyzing part of the cellulose. This type of pretreatment needs to be highly controlled to avoid excessive cellulose degradation which could result in an extensive loss of sugars. Pretreatment with brown rot fungi is common for woody feedstocks, but not so much for grasses. *Gleophyllum trabeum* was able to effectively pretreat sorghum bagasse, unlike *Serpula lacrymans, Postia placenta*, or *Fomitopsis pinicola* (Presley et al. 2018). Similarly, *S. lacrymans* was unable to significantly increase the amount of sugar recovered from sugarcane bagasse; however, it was effective in other herbaceous feedstocks, such as corn stover (Nurika et al. 2020).

Ascomycota fungi have also been evaluated for pretreatment of perennial grasses. Saccharification rates of over 40% were obtained with *Sporotrichum thermophile*, a soil fungus that is a proficient cellulose decomposer, after only 96 h of incubation time in *Saccharum* species (*Saccharum munja* and sugarcane bagasse) (Bala and Singh 2019). Similarly, the anaerobic fungus *Pecoramyces ruminantium* was used for saccharification of switchgrass, sorghum, energy cane, and a prairie mix, for further ethanol fermentation (Ranganathan et al. 2017). *Aspergillus niger* and *Trichoderma koningii* were used to successfully pretreat giant reed biomass, producing glucose yields of over 75% (Majeed et al. 2020).

Due to the high content of phenolic acid esters in grasses, the use of bacteria capable of breaking down the ester linkages has the potential to pretreat the grasses. Lactic acid bacteria that express the enzyme ferulic acid esterase have effectively increased the enzymatic digestibility of *Pennisetum sinese* (Li et al. 2020) and sorghum (Xie et al. 2021).

Pretreatment with microbial consortia for fermentable sugars

In most of the experimental work to develop pretreatment of grasses, a sterilization step is added to isolate the effect of the microorganism inoculated. However, for application at a commercial scale, sterilization is not economically feasible (Vasco-Correa et al. 2019b). In addition, the microorganisms used for pretreatment act, in nature, in consortia with others, often showing synergies that could benefit the pretreatment process. Thus, recent work has focused on pretreating unsterilized feedstock or using microbial consortia for the process (Vasco-Correa et al. 2016b, 2019a, 2022). The addition of white rot fungi has been able to control the propagation of other microorganisms during the wet storage of energy cane, as reflected by the higher dry matter loss in the control than in the fungal pretreatment (Cao 2016). However, *C. subvermispora* was quickly displaced by *Ascomycetes* fungi in successive fungal pretreatments of unsterilized *Miscanthus* (Vasco-Correa et al. 2022). Co-cultures of white rot fungi with other fungi or bacteria have shown high effectiveness in the production of fermentable sugars from lignocellulosic feedstocks, but the evaluation of those strategies in grasses is limited (González et al. 2021). Suhardi et al. (2013a) obtained an increase of about 60% in sugar yield and ethanol production by using a co-culture of *C. subvermispora* and *P. chrysosporium,* over each individual fungal strain, for the pretreatment of energy cane. Similarly, a higher ethanol yield from energy cane was obtained after pretreatment with a co-culture of brown and white rot fungi as compared to the pretreatment with the individual strains (Suhardi et al. 2013b).

Cell-free enzymatic pretreatment for fermentable sugars

Microbial pretreatment requires extensive incubation times to allow for microbial colonization and production of the required enzymes that alter the structure of the biomass. To circumvent this problem, pretreatment using the enzymes produced by the microorganisms in a cell-free reaction has been proposed (Table 2). Treatment with laccase enhanced the saccharification of *Saccharum* species (*Saccharum munja* and sugarcane bagasse) by twofold, achieving a sugar yield of about 55% (Bala and Singh 2019). Similarly, pretreatment with an enzyme extract of *Lentinus sajor caju* increased the sugar yield of Guinea grass (*Panicum maximum*) by 57% (de Freitas et al. 2021). Pretreatment with either laccase, lignin peroxidase, or manganese peroxidase did not enhance the digestibility of *Panicum prionitis*; however, pretreatment with enzymatic cocktails obtained from secretomes of white rot fungi *Pycnoporus sanguineus* and *Ganoderma applanatum* cultures were significantly more effective, reaching a sugar yield of over 45% with the latter species (Gauna et al. 2021). The results of cell-free enzymatic pretreatment are more limited and recent than those of microbial pretreatment with fungi or bacteria (Tables 1 and 2). In addition, most of the enzymatic pretreatment used crude enzymatic extracts instead of purified enzymes (Table 2). This is an indication that purified enzymes are not as effective since there is a well-known synergistic effect of lignocelulolytic enzymes. The pretreatment times are significantly shorter in enzymatic pretreatment; they are on a scale of hours instead of days or weeks (Tables 1 and 2).

Sugar-derived products from microbial pretreated grasses

Microbial pretreated biomass has been evaluated further for fermentation into solvents. Ethanol production from

Table 2 Enzymatic pretreatment of perennial grasses to release fermentable sugars

Grass	Enzyme type	Enzyme source	Glucose (or sugar) yield from pretreated grass	Percentage increase in glucose (or sugar) yield	Pretreatment time (h)	Reference
Panicum prionitis Ness	Fungal secretome	*Ganoderma applanatum* (white rot fungi)	17 to 20%	1107 to 1350%	48	(Gauna et al. 2021)
	Fungal secretome	*Pycnoporus sanguineus* (white rot fungi)	2 to 8%	1900 to 7800%	48	
Miscanthus	Bacterial secretome	*Bacillus* spp.	31%	62%	48	(Guo et al. 2017)
	Bacterial secretome	*Bacillus* spp.	97%	113%	48	(Guo et al. 2019)
Sugarcane bagasse	Laccase	*Ganoderma lucidium MDU-7* (white rot fungi)	55%	1733%	6	(Bala and Singh 2019)
Munja grass	Laccase	*Ganoderma lucidium MDU-7* (white rot fungi)	57%	2750%	6	(Bala and Singh 2019)
Guinea grass	Laccase crude extract	*Lentinus sajor-caju* (white rot fungi)	57%	21%	6	(de Freitas et al. 2021)

switchgrass increased by up to threefold after pretreatment with the white rot fungus *Pleorotus ostreatus* (Slavens et al. 2019). Fungal pretreated Napier grass with *P. chrysosporium* generated a similar ethanol yield than alkali pretreated grass, even though the glucose yield was 1.6 times higher with the alkaline pretreatment (Liong et al. 2012). Pretreatment with the white rot fungus *Trametes villosa* increased the ethanol yield from sugarcane bagasse by twofold (Hartmann et al. 2022). Yoon et al. (2019) produced ethanol from unsterilized sugarcane bagasse with a co-culture of the white rot fungus *P. sanguineus* and the fermentative yeast *Saccharomyces cerevisiae*. The fungus *Fusarium moniliforme* was used to produce about 6% of the ethanol theoretical yield from Napier grass in a consolidated bioprocess for ethanol production, which combined pretreatment/delignification, saccharification, and fermentation in one operation with one microorganism (Fig. 2) (Lao et al. 2022).

Fungal and bacterial pretreatment have been used to improve the fermentability of grasses into other solvents. The fermentability of switchgrass and *Miscanthus* into

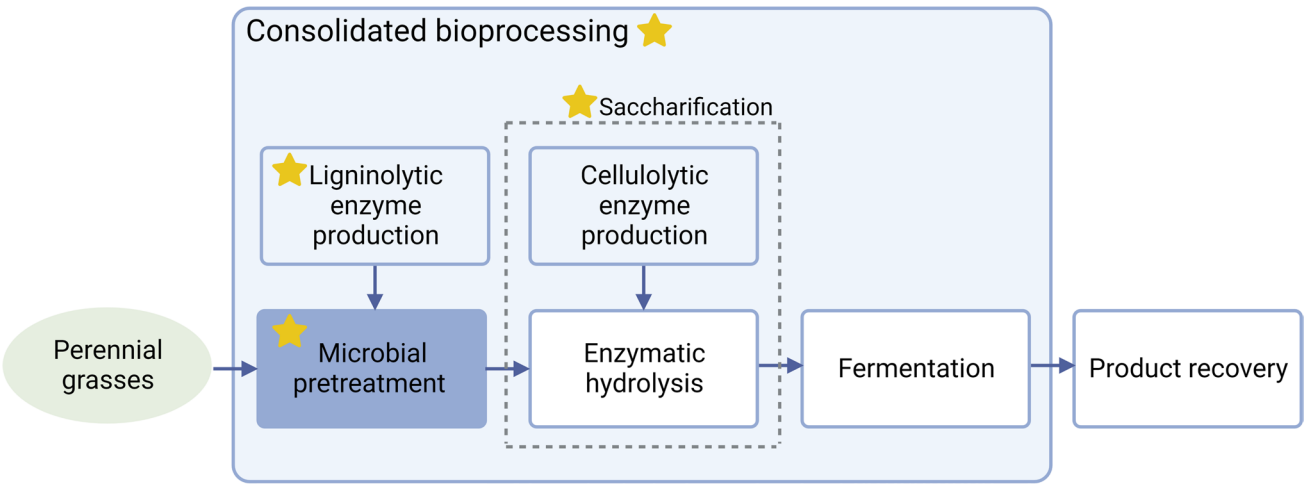

Fig. 2 Microorganisms (fungi and bacteria) can be used to improve the conversion of perennial grass lignocellulose into fermentation products. The yellow stars show the processes where microorganisms can be used in sugar-based grass biorefining beyond the typical uses in cellulolytic enzyme production and fermentation. These include the actual microbial pretreatment, production of ligninolytic enzymes for biomass delignification, direct saccharification of the biomass, and consolidated bioprocessing that combines delignification, saccharification, and fermentation. Created with BioRender.com

butanol was enhanced sevenfold to ninefold through fungal pretreatment with *P. chrysosporium* (Yao and Nokes 2014) and *C. subvermispora* (Vasco-Correa 2017). The cellulolytic bacterium *Fibrobacter succinogenes* was used for successful biological saccharification of *Miscanthus*, which was further fermented into butanol with results comparable to those of thermal treatment (Raut et al. 2019). Successive fungal treatments were used for both pretreatment and simultaneous saccharification and fermentation (SSF) of Napier grass into ethanol, using *Aspergillus niger* or *P. chrysosporium* for pretreatment, and *Neurospora sitophila* for SSF (Taufikurahman et al. 2020), showing how both the cellulolytic and ligninolytic capacities of fungi can be exploited at different stages of the biomass conversion.

Microbial pretreatment of grasses for biogas production

Anaerobic digestion (AD) is a mature technology that uses complex microbial communities in anoxic environments to convert organic matter into biogas, composed mostly of methane and carbon dioxide. The methane in the biogas can be burnt for heat and power or upgraded and used as renewable natural gas. AD has been extensively used as a technology for the management of organic waste, but its potential for bioenergy production has been increasingly exploited (Vasco-Correa et al. 2018). AD can be performed using a wide variety of feedstocks, including manure, sewage sludge, food waste, and agricultural wastes. However, lignocellulosic feedstocks have been of increasing interest to expand AD due to their abundance. In Germany, over 30% of the AD plants add grasses as part of their feedstock (Rodriguez et al. 2017).

Perennial grasses have been anaerobically digested in different conditions, either alone or in co-digestion with other feedstocks. However, their high recalcitrance to biological degradation limits the potential methane yield. The first step in the AD process is the hydrolysis of the grass polysaccharides into simple sugars, which are then converted into volatile fatty acids and finally into methane and CO_2. Due to the recalcitrance of lignocellulose, the rate-limiting step tends to be the initial hydrolysis, which constrains the biomethane potential of perennial grasses. For instance, a conversion of less than 25% of the polysaccharides (cellulose and hemicellulose) from switchgrass was obtained when the grass was anaerobically digested in both liquid- and solid-state conditions for 30 days. The resulting low methane yield of under 120 L/kg of volatile solids (VS) was similar to those of woody feedstocks (Brown et al. 2012). Similarly, *Miscanthus sinensis* showed a methane yield of 110 L/ kg of VS after 30 days of AD (Vasco-Correa and Li 2015), while *Miscanthus floridulus*' methane yield was about 200 L/kg VS after the same digestion time (Fu et al. 2018).

Pretreatments have been used to enhance the digestibility of the perennial grasses and thus increase the methane production in their AD. This includes thermochemical pretreatments such as hot water pretreatment, alkaline pretreatment, and acid pretreatment. Fu et al. (2018) significantly increased the methane yield from *Miscanthus* from 10 to 41%, by using different thermochemical pretreatments. The most effective pretreatment was hydrogen peroxide (2% H_2O_2) under alkaline conditions, which degraded more than half of the lignin content of the *Miscanthus* and achieved methane yields of over 320 L/kg VS (Fu et al. 2018). *Miscanthus* x *giganteus*, *Sida hermaphrodita*, and sorghum were unable to produce any biogas under the conditions studied by Michalska et al. (2012) and coworkers, but methane yields up to 252 L/kg VS were obtained after treatment with Fenton's reagent, which produced a lignin degradation of 30–68%.

Microbial pretreatments have also been explored to increase the methane yield from perennial grasses (Table 3). The conditions of microbial pretreatment, such as the mild temperature and the little to no added chemicals are usually more compatible with those of AD. Microbial pretreatment usually requires longer reaction times, and thus is usually performed during storage of the grasses. Pretreatment with the white rot fungus *Flammulina velutipes* raised the methane yield of tall wheat grass by 134–280%, while degrading 22% of its lignin content (Lalak et al. 2016; Kasprzycka et al. 2018). *Pleurotus ostreatus* pretreatment of giant reed harvested in winter increased its methane yield by 34%, while only a 13% increase was obtained for giant reed harvested in fall (Piccitto et al. 2022). The white rot fungus *Ceriporiopsis subvermispora* increased the methane production from anaerobic digested *Miscanthus* harvested in spring by 25% (Vasco-Correa and Li 2015). However, a similar process was unsuccessful for *Miscanthus* harvested in the fall (Vasco-Correa and Li 2015), or for giant reed (Liu et al. 2016c). Pečar and Goršek (2020) also showed a negligible increase in methane yield for *Miscanthus* pretreated with the white rot fungi *Pleurotus ostreatus* and *Trametes versicolor*, and Narinthorn et al. (2019) found a minimal increase in methane yield with fungal pretreatment of Napier grass with *Pleurotus sajor-caju*. Piccitto et al. (2022) observed a reduction in methane yield from giant reed after pretreatment with the white rot fungus *Irpex lacteus*, which was attributed to the simultaneous degradation of holocellulose with the delignification, which reduced the overall digestibility of the grass biomass.

Other fungi besides white rot fungi have been used to pretreat grasses. An *Ascomycota* fungus from the genus *Xylaria* enhanced the methane yield of some varieties of Napier grass by over twofold, while having a negligible effect on other Napier grass varieties and sugarcane leaves (Intasit et al. 2022). Bacteria have also been used to enhance

Table 3 Microbial pretreatment of perennial grasses to enhance biogas production

Grass	Microorganism species	Methane yield (L/kg VS)	Percentage increase in methane yield	Pretreatment Time (d)	Reference
Switchgrass	*Clostridium thermocellum*	280	17%	20	(Zheng et al. 2018)
Miscanthus	*Pleurotus ostreatus**	65	− 7%	21	(Pečar and Goršek 2020)
	*Trametes versicolor**	51	− 28%	21	
	*Ceriporiopsis subvermispora**	150 to 220	− 15 to 25%	28	(Vasco-Correa and Li 2015)
Giant reed	*Pleurotus ostreatus**	104 to 131	6 to 42%	30	(Piccitto et al. 2022)
	*Irpex lactus**	74 to 77	− 24 to − 16%	30	
	*Ceriporiopsis subvermispora**	100 to 125	− 33 to − 8%	30	(Liu et al. 2016c)
	Ensilage (naturally occurring lactic acid bacteria)	160 to 180	10 to 14%	30	
Napier grass	*Xylaria* sp. BCC 1067	247 to 862	48 to 147%	28	(Intasit et al. 2022)
	*Pleurotus sajorcaju**	259 to 303	13 to 32%	14	(Narinthorn et al. 2019)
	Microbial consortia (thermophilic bacteria enriched from compost)	259	17%	21	Wen et al. (2015)
	Microbial consortia (fungal and bacteria from plant litter, including *Coprinus cinereus* and *Ochrobactrum* sp.)	279	39%	21	
	Microbial consortium (mesophilic bacteria)	247	49%	21	
Tall wheat grass	*Flammulina velutipes**	135 to 181	7 to 280%	28	(Lalak et al. 2016; Kasprzycka et al. 2018)
Sugarcane bagasse	*Xylaria* sp. BCC 1067	95	279%	28	(Intasit et al. 2022)
Paragrass	*Coprinopsis cinerea*	311	− 15%	30	(Nuchdang et al. 2015)
	*Polyporus tricholoma**	313	− 15%	30	
Grass of verge	*Phanerochaete flavido-alba**	137.5	6%	21	(López et al. 2013)
Giant grass	Microbial consortium (commercial compost liquid inoculant)	275	23%	5	(Wang et al. 2021b)
	Microbial consortium (commercial straw composting inoculant)	279	24%	5	
	Microbial consortium (cow manure)	265	16%	5	

*Confirmed white rot fungus

the methane yield from perennial grasses. Pretreatment with *Clostridium thermocellum* improved the methane production from switchgrass by 20%, while an increase of 25% was obtained by using this anaerobic bacterium for bioaugmentation of the AD process, achieving methane yields of about 280–290 L/kg VS after 30 days (Zheng et al. 2018). Similarly, pretreatment with varied microbial communities boosted the methane yield of giant grass by 16–25% (Wang et al. 2021b); and co-fermentation with rumen bacteria increased the methane production from switchgrass by 27–37% (Zheng et al. 2019). Pretreatment with a mixed culture microbial sludge increased the methane yield from a co-digestion of Napier grass and elephant dung by almost 2 times (Rangseesuriyachai et al. 2022). A lignocellulolytic microbial consortium was enriched from forest compost soil to enhance the biodegradability of Napier grass for biogas production (Kanokratana et al. 2018). Wen et al. (2015) enhanced the methane yield from Napier grass 1.3–1.5 times with microbial consortia-based pretreatment.

Lignin degradation, and the consequent increase in feedstock digestibility, appears to be the main effects of most pretreatments that enhance methane production from perennial grasses effectively. Thus, lignin-degrading enzymes such as laccases and lignin peroxidases have been used directly to pretreat lignocellulosic feedstocks. This pretreatment has been mildly effective with other lignocellulosic feedstocks such as flax and willow; however, it was unsuccessful for *Miscanthus* (Schroyen et al. 2015).

Microbial pretreatment of grasses for animal feed

Grasses and grain crops broadly fulfill the nutritional demands of ruminant livestock around the globe. Digestible fiber fractions of these feed materials (i.e., starch, cellulose, and hemicellulose) are depolymerized into sugars, which are then converted into methane and volatile fatty acids (VFAs)—the major source of energy supply for ruminants. Such transformations of plant material into VFAs are

utterly dependent on a complex, highly dynamic microbial community inside the first stomach of ruminants (i.e., the rumen) and known as rumen fermentation (Gruninger et al. 2019). Ruminal microorganisms cannot break down lignin, resulting in the limited digestibility of lignin-rich perennial grasses compared to the more energy-dense feed grains (corn, barley, oats, etc.). In fact, some authors have stated that the proportions of each one of the coniferyl alcohol, p-coumaryl alcohol, and sinapyl alcohol units in lignin might differentially affect feed digestibility for ruminants (Zhong et al. 2021). Despite digestibility challenges and disputed higher greenhouse gas emissions of grass-fed livestock (Clark and Tilman 2017; Lynch and Pierrehumbert 2019), perennial grasses have become the dominant nutritional source for ruminants in some regions of the world (Norton et al. 2016), and labels such as "grass-fed" or "grass-finished" are becoming increasingly common in beef industry some markets.

A variety of microbial-based technologies have been used over the years to improve the digestibility of grasses to be used as lignocellulosic feed. Approaches include traditional ensiling (e.g., autochthonous microflora); bio-augmented ensiling (e.g., autochthonous microflora plus inoculation of lactic acid bacteria); and use of exogenous enzymes.

Ensiling: crop preservation technology and its effects on feed digestibility

Ensiling has been historically considered a cost-effective forage crop preservation method that is widely implemented in non-temperate regions to provide a year-round supply of animal feed. During traditional ensiling, wet solid crop particles are compressed to reduce air space and stored under airtight conditions for extended periods. This induced oxygen-depleted environment supports the development of indigenous anaerobic microflora, mainly lactic acid bacteria, which metabolize free carbohydrates into organic acids during growth. Organic acid production and accumulation lead to a decrease in pH values, which concomitantly with anoxic conditions, limit the development of filamentous fungi, yeast, and other bacteria (Wang et al. 2023). The limited proliferation of spoilage-inducing organisms has been considered of utmost importance because they may otherwise lead to significant unwanted losses of structural polysaccharides during crop storage (Ambye-Jensen et al. 2013). Therefore, successful ensiling processes yield a low-pH material known as silage, which shows two main characteristics: (1) minimal nutritional losses compared to the original crop and (2) some increase in feed digestibility due to compositional changes (i.e., lignocellulose hydrolysis) promoted by prolonged acidic storage conditions and endogenous enzymatic action by microbial or plant enzymes (Desta et al. 2016; Baldini et al. 2017).

Recent research indicated that ensiled-chopped elephant grass (Napier grass) presented significantly higher nutrient digestibility indicators compared to the fresh whole forage, which promoted voluntary feed consumption by cows potentially increasing dairy production (Pratama et al. 2021). Similar results were obtained by Bureenok et al. (2012) who reported improved digestibility of Napier grass after ensilage processes both with and without additives. Interestingly, the addition of external lactic acid bacteria (bioaugmentation) had an inconsequential effect on digestibility compared to the control silage (silage with no additives); however, molasses addition significantly improved feed quality and intake by about 1.4 times. It was hypothesized that molasses promoted the proliferation of heterofermentative lactic acid bacteria during the ensilage period that released acids other than lactic acid, and that these improved the stability of silage against spoilage organisms when exposed to aerated conditions. Feed quality of grass silages has been frequently shown to vary with the extent of fermentation and acid production, which is largely conditioned by the microbial community (Dong et al. 2020) and the grass properties including dry matter, water soluble carbohydrates, and neutral detergent fiber; these properties are in turn dependent on plant´s maturity (Liu et al. 2016a; Li et al. 2021). For instance, Weiby et al. (2022) showed that round grass bales with high differences in composition regarding digestible and indigestible fibers had high variations in acid profiles produced during 70 days of ensiling. These variations were later associated with the potential of methane emission during ruminants' metabolism.

Joining animal feed scientists, ensiling technology has gained the attention of researchers working on biofuel and biochemical production from lignocellulosic feedstocks as it offers a reliable long-term storage approach with simultaneous pretreatment of biomass components under mild conditions, such as ambient temperature and pressure (Li et al. 2018). It also eliminates the need for energy-intensive steps such as drying or sophisticated storage equipment (Williams and Shinners 2014). Therefore, ensilage has been used as a pretreatment step for other non-feed-oriented processes such as those focused on biohydrogen and methane production from different grasses (Liu et al. 2016b; Prapinagsorn et al. 2017, 2018; Zhao et al. 2017b; da Borso et al. 2018; Jomnonkhaow et al. 2021).

Effects on feed digestibility by exogenous enzymes

The application of exogenous enzymes to improve the digestibility of lignocellulose-rich feedstocks (mainly crop residues) for feeding ruminant livestock has been extensively studied and has been recently reviewed elsewhere (Tirado-González et al. 2021; Carrillo-Díaz et al. 2022). The most common sources of enzymes for cell wall component

hydrolysis from plant materials are fungi, including brown rot, soft rot, and white rot species (Sista Kameshwar and Qin 2018). In particular, white rot fungi are known for their production of a variety of extracellular non-specific enzymes capable of modifying all lignocellulose components and had been widely used for biorefining of crop residues, as discussed in the previous section. White rot fungi have also been used to improve the digestibility of herbaceous feedstock for animal feed (Nayan et al. 2017), including some perennial grasses (Akin et al. 1993, 1995). However, there is limited information regarding the recent implementation of white rot fungi for treating grasses for ruminant feed.

Recently reported literature evaluating fibrolytic enzyme extracts (FEE), as they are commonly known, implements FEE derived from a soft rot fungus, *Trichoderma reesei*, to treat tropical grasses and determine their nutritional properties changes. Researchers determine the enzymatic dosages that increase the degradability of Tifton-85 hay (*Cynodon* spp.), Aruana grass (*Panicum maximum*), and Buffel grass (*Cenchrus ciliaris* L.) during in vitro assays (Sakita et al. 2020). In further studies, they observed a significant increase in digestibility and a reduction of greenhouse gas emissions by lambs fed with FEE-treated grass, as compared to the untreated grass controls, highlighting the innocuity of the fungal extracts on animal health (Sakita et al. 2022). Increased digestibility is not always achieved when applying exogenous enzymes. Several authors have found no significant effects of enzyme addition on the final digestibility of fresh grass even when reducing particle sizes, which would increase the enzyme accessibility to the lignocellulose components (Assoumaya et al. 2007). The variability in results has been attributed to the complex interaction of multiple variables that significantly affect enzyme action, such as the appropriate dosage of enzyme extract, the types of enzymes present in the extract, the physicochemical conditions for the enzymatic reaction (pH, temperature, water activity), and feedstock composition (lignin, cellulose, hemicellulose, pectin) and particle size (Beauchemin et al. 2003; Carrillo-Díaz et al. 2022).

Microbial pretreatment of grasses for other uses

Microbial pretreatment has also been used to improve the densification and further thermochemical conversion of biomass, since fungal pretreatment has the potential to enhance the properties of grass pellets. White rot fungal pretreatment with *T. versicolor* increased the compressive strength of *Miscanthus* pellets (Kalinoski et al. 2017). Similarly, the tensile strength of switchgrass pellets increased with white rot fungi treatment and the researchers hypothesized that the fungal pretreatment released inherent binders of the lignocellulose (Olughu et al. 2021). However, it is also well-known that mycelium can act as a binder of biomass, since it has been extensively used for the production of fungal composites (Jones et al. 2020). Thus, it is possible that the binding effect was caused by the mycelium that grew in the switchgrass. Yet, shorter fungal pretreatment times in similar conditions decreased the pellet quality, in terms of tensile strength, porosity, and pellet density (Olughu et al. 2022).

Thermochemical processing can also benefit from the modifications imparted by microbial pretreatment of herbaceous biomass (Gu et al. 2021). Fungal and bacterial pretreatment enhanced the sorption properties of *Miscanthus lutarioriparius* biochar produced through pyrolysis after the pretreatment (Xu et al. 2022). However, pretreatment with the white rot fungus *P. chrysosporium* did not improve the hydrothermal liquefaction of switchgrass, as compared to conventional pretreatments (Embry 2018).

Traditionally, microorganisms have been used for pulping and bleaching fibers (Kumar et al. 2017). Biopulping is usually performed with ligninolytic microorganisms such as white rot fungi or their enzymes to remove hemicellulose and lignin and improve the quality of the cellulose pulp (Singh et al. 2010; Kaiquan et al. 2021). Even though grass fibers are not as commonly used as other feedstocks in the pulp and paper industry, some studies have used microbial pretreatment of perennial grasses to improve pulping and bleaching. A recent study has developed microbial communities based on the rumen of elephants and has applied them for the bleaching of sugarcane bagasse for cellulose fiber extraction (Sriwong and Sukyai 2022). Similarly, pretreatment with xylanases from *Bacillus australimaris* and other microorganisms improved the physical and chemical properties of bamboo (*Bambusa tulda*) pulp (Dutta et al. 2020) and enhanced the cellulose extraction from sugarcane bagasse (Vanitjinda et al. 2019) and cellulose nanocrystals from energy cane (Meesupthong et al. 2021). All these pretreatments reduced the use of chemicals in the bleaching process (Vanitjinda et al. 2019; Dutta et al. 2020; Sriwong and Sukyai 2022).

Coproducts of microbial pretreatment of grasses

As part of the biorefinery approach, different molecules can be produced and further recovered after the growth of microorganisms in plant biomass, either as products of the deconstruction of the lignocellulosic material or as microbial metabolites. Enzymes produced by the microorganisms used for pretreatment could be recovered and used for other applications. For example, ligninolytic enzymes from white rot fungi can be used in the pulp and paper industry and in bioremediation applications. Cellulolytic enzymes, which can be used for holocellulose saccharification, can be produced by fungi and bacteria grown in grass biomass (Menegol et al. 2017). Microorganisms express different enzymes according to the substrate used for their growth (i.e., the type of biomass they are consuming) (Rashed

Alaradi 2017). Thus, enzyme cocktails produced in solid-state culture during fungal pretreatment of grasses are more likely to be highly effective in further enzymatic treatment of similar feedstocks, as shown by Cianchetta et al. (2017).

Grasses are rich in hydroxycinnamic acids (HCAs) such as ferulic acid and p-coumaric acid, which have a high potential as antioxidants and platform chemicals in green chemistry and can generate added-value products for the biorefinery. Rumen microorganisms produce esterases that release HCAs, which can be later catabolized by the microorganisms (Wang et al. 2022). The presence of HCAs can inhibit microorganisms and limit the bioconversion of grasses into both biogas through AD and ethanol through enzymatic saccharification and fermentation (Balasundaram et al. 2022; Wells et al. 2022). However, HCAs could be extracted from grasses for conversion and commercialization. Bichot et al. (2022) extracted HCAs from *Miscanthus* with a combination of enzymatic and microwave pretreatment, using a xylanase-based cocktail. Suzuki et al. (2022) extracted HCAs from grasses with alkaline pretreatment and then used an engineered bacterium (*Pseudomonas putida*) to convert the mix of HCAs into a single intermediate molecule, in a process of microbial funneling, while leaving a biomass with higher enzymatic digestibility. They evaluated the process for two independent intermediate molecules, 2-pyrone-4,6-dicarboxylic acid or PDC and (4S)-3-carboxymuconolactone (4S-3CML), which are building blocks for biopolymers (Suzuki et al. 2022).

Oligosaccharides from cellulose and hemicellulose are important prebiotics with increasing markets that can be generated by selective degradation of polysaccharides. Xylanases have been used to release xylo-oligosaccharides from perennial grasses (Kulkarni et al. 2012). Zhou et al. (2020) used enzymatic treatment for esterification to generate cello-oligosaccharides from switchgrass and reed, achieving a product purity of over 70%.

Conclusions and future perspectives

Microbial pretreatment has been extensively used to enhance the biodegradability of perennial grasses for animal feed use or further processing in biorefineries. Fungal pretreatment is still the most common microbial pretreatment for lignocellulosic biomass, but its application to perennial grasses is not as extensive as it is to woody feedstocks, because most biotechnologically-relevant fungi are better adapted to wood than to herbaceous biomass (Fig. 3). Nevertheless, highly

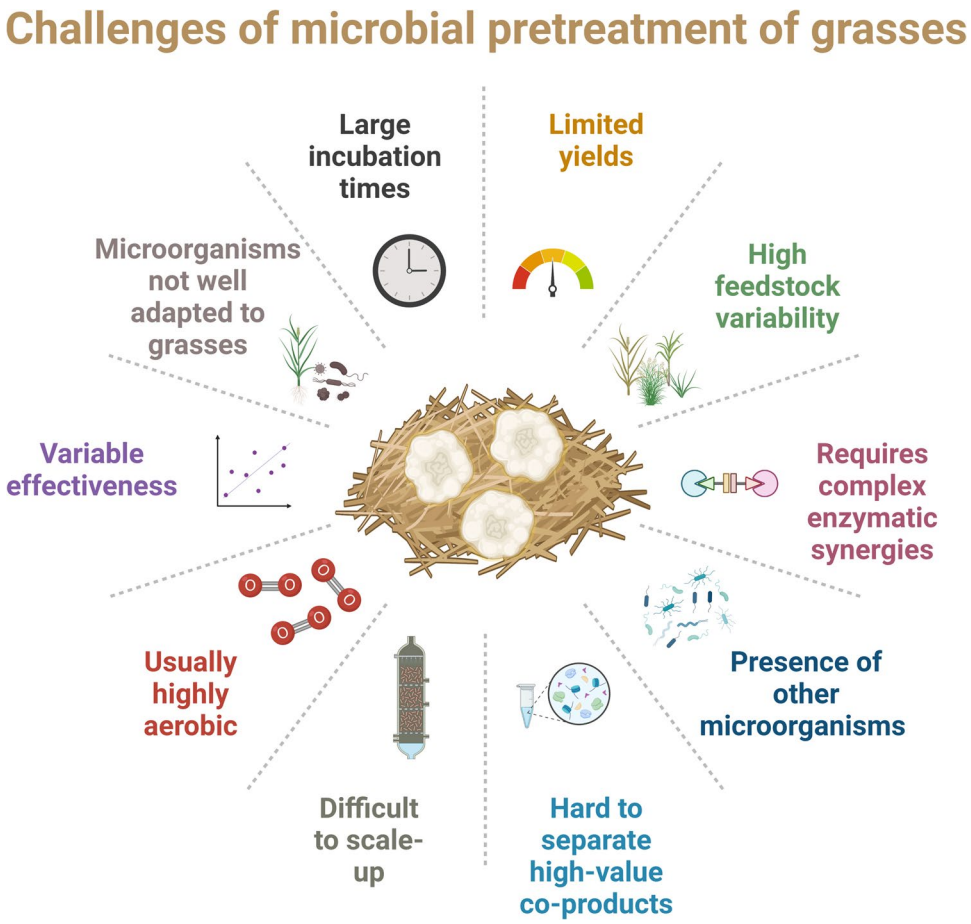

Fig. 3 Main challenges for the development and implementation of microbial pretreatment for herbaceous biomass for biorefining. Created with BioRender.com

effective fungal pretreatments have been developed for perennial grasses that significantly enhance their digestibility and allow for conversion into high-value products. Bacterial pretreatment application for grasses is more limited, but cell-free enzymatic pretreatment with both bacterial and fungal enzymes has increased significantly in recent years. Enzymatic pretreatment has shown effectiveness when crude enzyme extracts are used, rather than purified enzymes. The efficacy of purified enzymes in pretreatment is limited because targeting the degradation of a unique component of the cell wall is insufficient to significantly disrupt the complex structure of lignocellulose. The biodegradation enhancement of grasses depends on the action and synergy of several enzymes (Fig. 3) because the recalcitrance of the grasses is determined by a series of complex interconnected physicochemical factors that protect the plant against pathogenic biodegradation, and which include the content and arrangement of cell wall components; the heterogeneity, crystallinity, degree of polymerization, and branching of the cell wall polymers; the presence of aromatic compounds with complex degradation pathways; and the porosity, among many others.

Processes that use natural microbial communities such as ensiling have been extensively used to enhance the digestibility of grasses; however, their application has been more common for low-value products such as animal feed. This is because the material resulting from ensiling with natural microbiomes is more prone to variability and thus more difficult to convert into high-value products, which usually required consistency in the feedstock properties. Recent trends in using either naturally occurring or inoculated microbial consortia in microbial pretreatment for higher-value biorefining products have underscored the applicability of microbial pretreatment to unsterilized grasses under wet-storage conditions. The development of reliable and controllable microbial pretreatment of unsterilized grasses could enhance its scalability and potential for commercial application. Studies that engineer microbial consortia from a bottom-up approach or tailor and enrich existing microbial communities using a top-down approach could both provide pathways for further improvement of the effectiveness and applicability of microbial pretreatment for biorefining, by taking advantage of natural microbial synergies and redundancies to generate robust systems that are more reliable for commercial scales.

Microorganisms have the capacity to produce a range of metabolites with varied uses during the microbial pretreatment process. These metabolites have included ligninolytic and cellulolytic enzymes, acids derived from the grass biomass such as hydroxycinnamic acids, and products derived the polysaccharide fractions such as oligosaccharides. These products have the potential to be excellent additional revenue streams for biorefineries and contribute to the economic feasibility of these operations. The growth of fungi and bacteria in grass biomass could produce many other added-value metabolites while simultaneously enhancing its digestibility, and this research area is still highly unexplored since the focus has been mostly on reducing the recalcitrance to improve hydrolysis. Furthermore, the process conditions that favor the metabolites' production, and the processes for their extraction, recovery, and purification need to be studied. Since most microbial pretreatment is performed in a solid state, recovering some of these chemicals in an economically feasible manner represents a significant challenge to overcome, because of the resulting complex mixture of metabolites and the separation of those from the microbial biomass and the grass feedstock.

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Author contribution JVC conceived the paper. JVC and AZC performed the literature review and wrote the manuscript. AZC, JGL and JAPT critically reviewed the manuscript. All authors read and approved the manuscript.

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Code availability Not applicable.

Data Availability All data generated or analysed during this study are included in this published article.

Declarations

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Competing interests The authors declare no competing interests.

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